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Three new species of *Grylloblatta* Walker (Insecta: Grylloblattodea: Grylloblattidae), from southern Oregon and northern California

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Abstract

***Grylloblatta oregonensis* new species, *Grylloblatta siskiyouensis* new species,** and ***Grylloblatta marmoreus* new species** are described from the Klamath Mountains region of Oregon and California, U.S.A. Two species were found at Oregon Caves National Monument, with *G. oregonensis* inhabiting the dark zone of caves and *G. siskiyouensis* inhabiting surface habitat and the twilight zone of caves. The third species, *G. marmoreus,* is known from Big Foot Cave and Planetary Dairy Cave, Marble Mountains, California. These three species are recognized on the basis of morphological characters and distinguished from nearby *Grylloblatta* species. Analysis of genetic data from the cytochrome oxidase subunit II gene supports the morphological diagnosis of these three species as unique lineages and confirms their genetic divergence from other ice-crawler populations found in Oregon and California.

Key words: Oregon Caves National Monument, Marble Mountains, endemic species, ice-crawler, grylloblattid

Introduction

In 1913, Walker discovered and subsequently described *Grylloblatta campodeiformes* from Banff, Canada and established the family Grylloblattidae (1914). Since that time, 10 additional species and two subspecies (Caudell 1924, Gurney 1937, 1953, 1961, Kamp 1963, 1979, Silvestri 1931) have been described in North America, ranging from the Sierra Nevada, California to the Cassiar Mountains in northern British Columbia. Grylloblattids are notoriously rare throughout their range and the lack of adult specimens has resulted in numerous references to isolated populations that have remained undescribed for half a century (Gurney 1953, 1961). The rarity of grylloblattids has also raised concern over their conservation status (IUCN 2010, Jarvis & Whiting 2006).

A need currently exists to update the taxonomy and distributional knowledge of the grylloblattids, particularly in light of recent phylogenetic work identifying several unique genetic lineages that might represent new species of *Grylloblatta* (Jarvis & Whiting 2006, Schoville & Roderick 2010). Here I examine adult specimens from Oregon Caves National Monument and the Marble Mountains, California, and provide a morphological assessment that recognizes three new species. Additionally, I use DNA sequence data to assess the genetic divergence among these three species and confirm their status as unique lineages relative to other grylloblattids from Oregon and northern California.

Material and methods

Morphological analysis. This report is based on the study of adult female specimens from Oregon Caves National Monument, described here as representing two new species, and one adult male specimen from Marble Mountains, California. All specimens in the type series were collected directly into ethanol. Additional samples of grylloblattids from these localities were all juveniles and were not used in the morphological diagnosis, although they were assignable to species based on morphological and genetic criteria. Comparisons were made to museum specimens and published species descriptions. The institutional code CAS cited in the text represents the California Academy of Sciences, San Francisco, California, USA.

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Physical measurements were made with a reticle (EW-46800-21) mounted in a Cole-Parmer Stereozoom microscope (FF-48920-20**)**, or dial vernier calipers. Standardized measurements include:

Body length (BL): the distance from the clypeal (epistomal) suture to the insertion of the cerci.
Head length (HL): the distance from the clypeal suture to the pronotum.
Head width (HW): greatest width measured dorsally across the head.
Eye length and width (EL and EW): greatest length along the body axis and greatest width perpendicular to body axis
Interorbital Distance (ID): the shortest distance (dorsally) between the compound eyes
Antennomere 1 and 2 length and 2:1 ratio (Ant1L, Ant2L, AntRatio): length of antennomere 1, length of antennomere 2, and length of antennomere 2 divided by the length of antennomere 1.
Pronotum length and width (PL and PW): greatest length and width measured dorsally across the pronotum.
Legs: front, mid and rear legs measured for femur length (FL), tibia length (TL), tarsus length (TrL), and pre-tarsus length (PTrL).
Male subgenital plate length and width (SbgL and SbgW): length along the midline of subgenital plate measured from the last abdominal segment and width at the proximal base of the subgenital plate.
Male right and left coxopodite (gonacoxa) length and width (RCxL, RCxW, LCxL, and LCxW): length along midline and width across proximal base.
Female ovipositor length and width (OvL and OvW): greatest length from proximal base to distal tip of ventral valve of ovipositor and width across proximal base.
Cercus length (CL): length from insertion point to distal end.

Specimens were digitally photographed with a Canon Digital Rebel XT camera mounted on a dissecting microscope. Digital images were edited, cropped and scaled in Adobe Photoshop CS3. Specimen colors were determined according to Ridgway (1912), with color numbers reported in parentheses.

Genetic analysis. Five individuals were selected for genetic analysis. From Oregon Caves National Monument, two juveniles were sampled from *G. oregonensis* **n. sp.** and one from *G. siskiyouensis* **n. sp.** These specimens were easily assigned to species based on dorsal pigmentation of the head and thorax. For the Marble Mountains, a portion of the leg of the adult male type specimen and leg tissue of one juvenile from a nearby cave were sampled. A DNeasy tissue kit (Qiagen) was used to extract genomic DNA from the tissue samples. Approximately 790 base pairs of the cytochrome oxidase subunit II mitochondrial gene were amplified using universal primers (COII-F-leucine and COII-2-R-lysine; Svenson & Whiting 2004) in standard PCR conditions and sequenced in both directions. Sequences of other *Grylloblatta* specimens, including topotypic specimens from nearby type localities in California, were available from GenBank (Jarvis & Whiting 2006, Schoville & Roderick 2010). For comparison, I used genetic data from a single specimen from Oregon Caves (DQ457366) known to be dark in coloration, as well as samples from *G. barberi* Caudell (FJ918624), *G. gurneyi* Kamp (DQ457347-DQ457349), *G. chandleri* Kamp (FJ918575), *G. chirurgica* Gurney (DQ457364), and two samples that were putatively assigned by Jarvis and Whiting (2006) as *G. rothi* Gurney (DQ457341) and *G. sculleni* Gurney (DQ457368). Genetic distance was measured as the pairwise sequence divergence between each specimen, after correcting the substitution rate using the Kimura 2-parameter model (Kimura 1980). The pairwise differences between these taxa were then used to construct a neighbor-joining tree and 1000 bootstrap samples were used to assess statistical support for the topology. The consensus bootstrap values are shown at the nodes of the neighbor-joining phylogeny and branch lengths are proportional to the scale bar. A sample of *G. campodeiformes* (DQ457367) was used as an out-group in the construction of the tree.

Grylloblatta oregonensis new species

(Figs. 1A, 2A–B)

Type material. Holotype female in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M. N42.098 W-123.407 WGS84, Note: in dark zone of cave 15-VI-2010 J. Roth SDS10-007" [white label]/ "HOLOTYPE *Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [red label]; dark zone of cave, Oregon Caves National Monument, 42.098º North and -123.407º West, Josephine County, Oregon, U.S.A.

Other specimens. Juvenile in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M. 20-III-2010. Note: in the dark zone, drowned in a pool of water." [white label]/ "*Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [white label]. Juvenile in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M. 30-XI-2006" [white label]/ "*Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [white label]. Juvenile in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M. 11-VII-2008" [white label]/ "*Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [white label]. Juvenile in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M. 14-I-2009" [white label]/ "*Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [white label]. Juvenile in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M." [white label]/ "*Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [white label]. Penultimate male in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M. SDS10-003" [white label]/ "*Grylloblatta oregonensis* Schoville det. S.D. Schoville 2011" [white label].

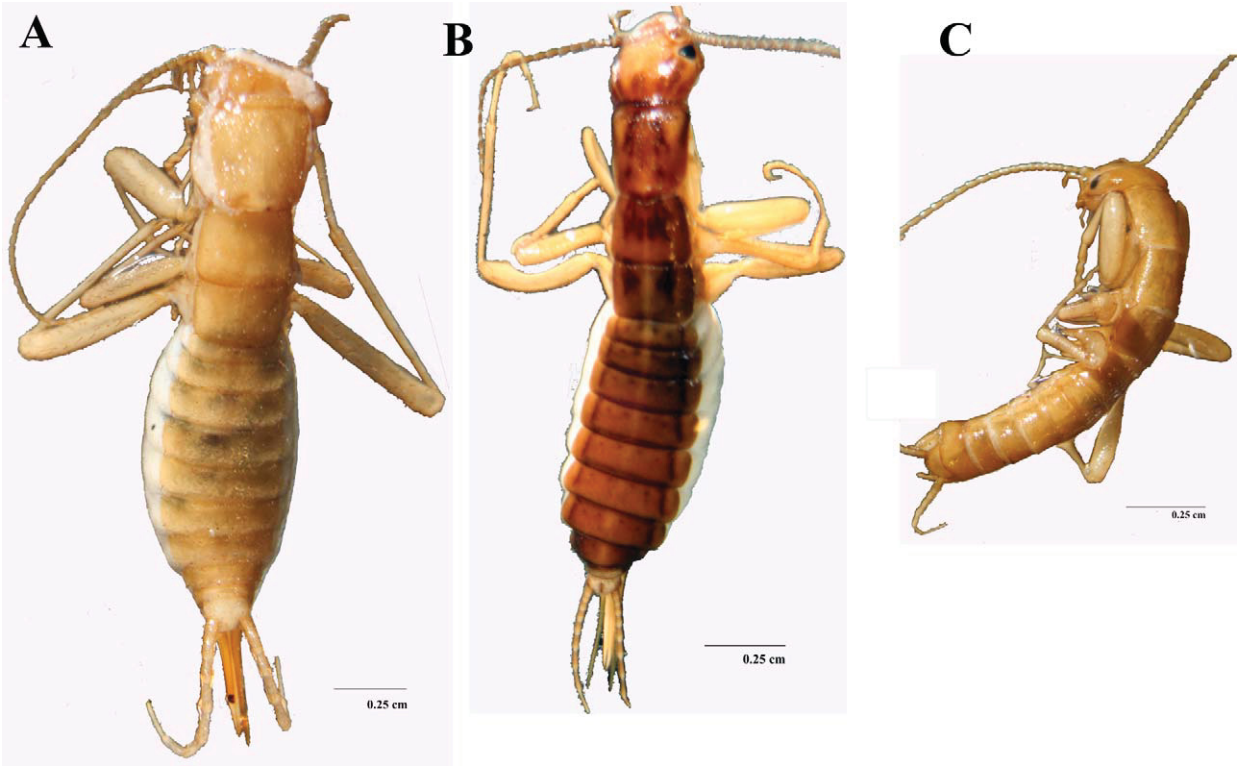

FIGURE 1. Differences in size and coloration observed in type specimens. A) *Grylloblatta oregonensis* **n. sp.** B) *G. siskiyouensis* **n. sp.** C) *G. marmoreus* **n. sp.**

Etymology. The specific epithet, *oregonensis*, is named for the state of Oregon in which the type locality, Oregon Caves National Monument is located.

Diagnosis. Adult females of this species can be distinguished from all other Nearctic *Grylloblatta* species by the following combination of character states: color buff yellow on dorsum and white ventrally; large body size (>1.4cm); long legs; fewer than 30 antennomeres; ratio of antennomere lengths 2 and 1 2.67; broad head; head slightly wider than pronotum; compound eyes large; pronotum square-shaped with flat posterior edge; long, narrow and weakly up-curved ovipositor; dorsal valve of ovipositor noticeably down-curved at tip; ovipositor half as long as cercus; cercomeres long. Holotype specimen with slight damage limited to the juncture of the pronotum and head on the left side (caused during transfer to alcohol).

Description of holotype female. Antennomere number on right antennae 28 and on left antennae 26. Compound eyes well developed, black. Interocular distance slightly smaller than pronotum width. Head width less than head length. Head slightly damaged by split in the exoskeleton and swelling tissue in the posterior end. Pronotum square-shaped with rounded corners, surface broad and flat, length greater than width, width at anterior and posterior ends similar, slight inward curve laterally, transverse sulcus at anterior end straight, posterior edge flat. Slightly damaged along anterior and left sides by a split in the exoskeleton and swelling tissue. Legs long and robust, same

yellowish color as dorsum with distinctive brown setae. On abdomen, ovipositor half as long as cercus. Ventral valve gradually becoming narrower and curving gently upwards towards distal end, lightly setaceous with short setae. Dorsal valves barely extending beyond ventral valve (<one-eighth total length) and at distal end curving downward. Dorsal valve coloration noticeably darkened along dorsal surface near proximal end. Cercal segments long, coloration of proximal ends amber yellow and distal ends white. Dorsal body color buff yellow (87), with amber yellow (84) head and pronotum, abdomen white, appendages lighter amber buff yellow, antennomeres and cercomeres buff yellow fading to white at distal ends, ovipositor salmon-orange (50). Juveniles sharing characteristic pale dorsal coloration on the head and pronotum, sometimes completely white.

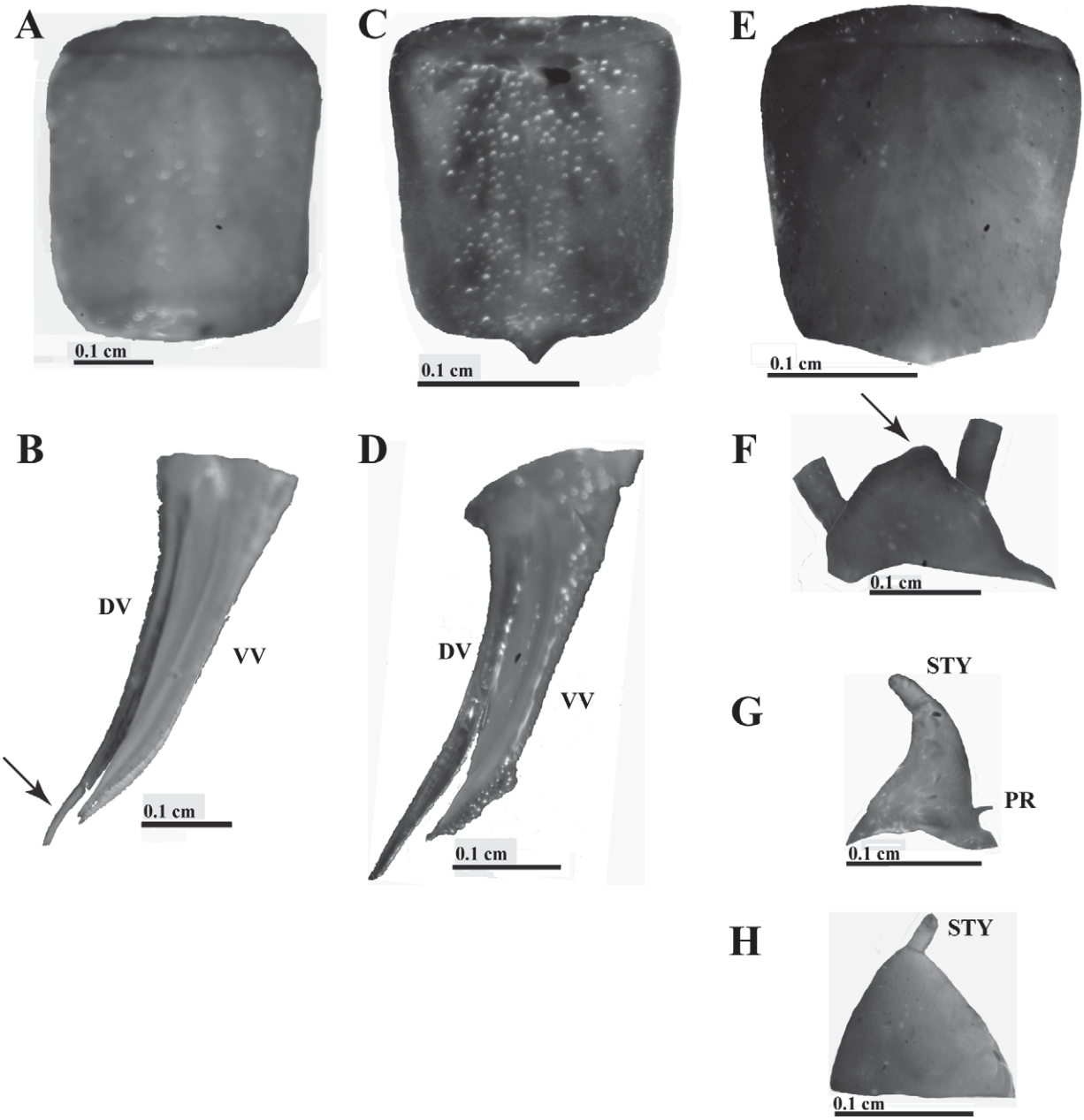

FIGURE 2. Diagnostic features of *Grylloblatta oregonensis* **n. sp.** include the A) square-shaped pronotum and B) dorsal valve (DV) of ovipositor with down-curved tip. Diagnostic features of *Grylloblatta siskiyouensis* **n. sp.** include the C) narrow pronotum with pointed posterior edge and D) ovipositor with dorsal valve (DV) extending beyond ventral valve (VV) by one-fifth the total length. Diagnostic features of *Grylloblatta marmoreus* **n. sp.** include the E) trapezoidal pronotum with soft triangular point at posterior end, F) subgenital plate with slight rounded tooth at apex, G) right coxopodite with sharply curved process (PR), and H) left coxopodite with short, stubby stylus (STY).

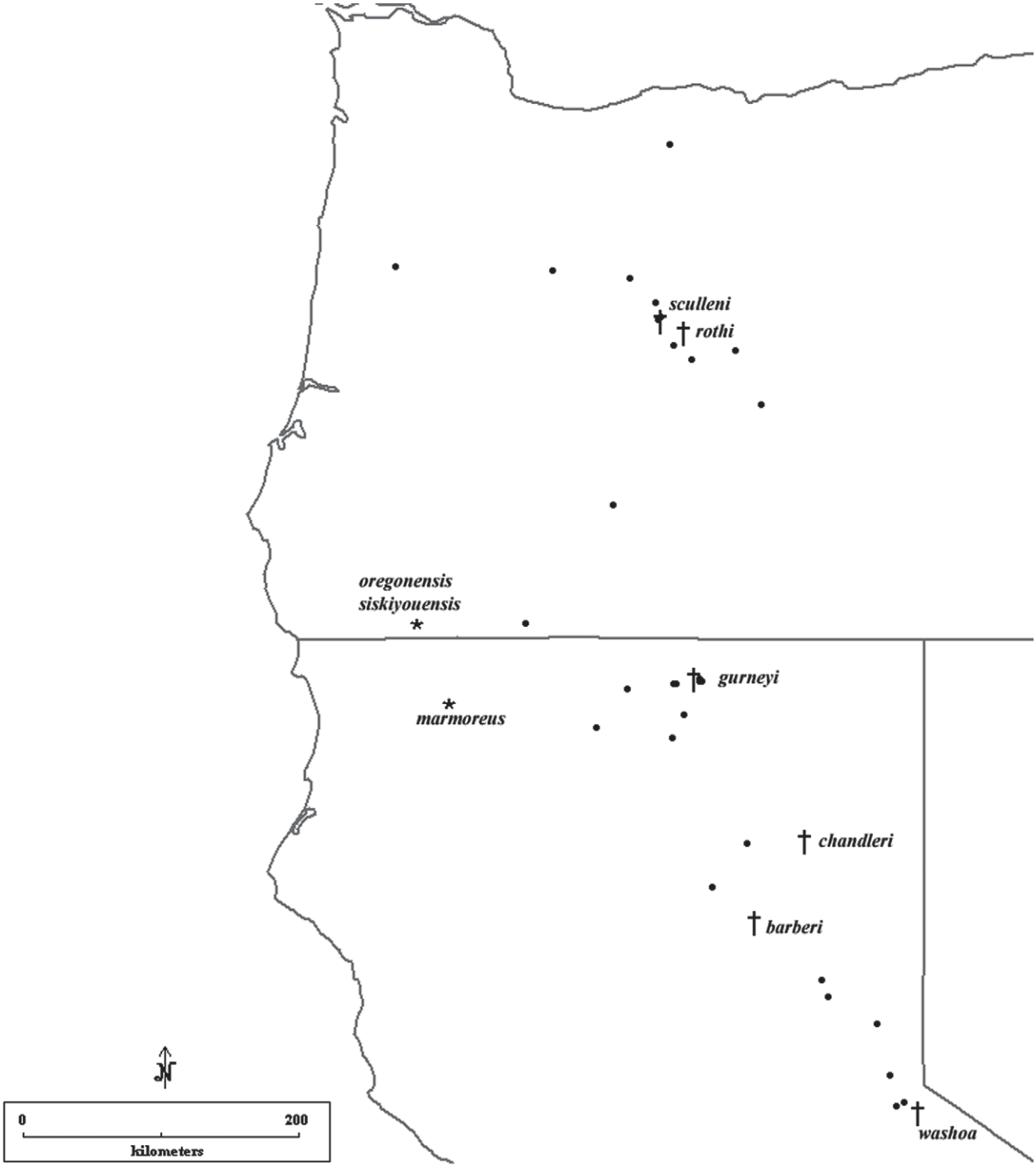

FIGURE 3. Geographical distribution of grylloblattid populations (dots) and type localities (crosses and asterisks) in California and Oregon, USA.

Measurements of holotype female (cm). BL 1.905, HL 0.476, HW 0.378, EL 0.103, EW 0.064, ID 0.325, Ant1L 0.024, Ant2L 0.064, AntRatio 2.67, PL 0.405, PW 0.349, FL front 0.564, FL mid 0.476, FL rear 0.635, TL front 0445, TL mid 0.476, TL rear 0.714, TrL front 0.119, TrL mid 0.095, TrL rear 0.278, PTrL front 0.476, PTrL mid 0.357, PTrL rear 0.397, OvL 0.516, OvW 0.1588, CL 1.032.

Description of other specimens. Juveniles share the characteristic pale dorsal coloration and are sometimes completely white.

Comparisons. *Grylloblatta oregonensis* **n. sp.** can be distinguished from *G. siskiyouensis* **n. sp.** by larger body size, buff yellow dorsal coloration, fewer number of antennomeres and larger antennomere 2:1 ratio (>2), longer

cercus to ovipositor ratio, longer and slightly tapered ventral valve of ovipositor, and slightly down-curved distal end of the dorsal valve of ovipositor. It can be distinguished from *G. marmoreus* **n. sp.** by the large, square pronotum with flat posterior edge, and relatively longer limbs. It can be distinguished from *G. rothi* by its wider head and pronotum, longer limbs, and slightly less up-curved ventral valve of ovipositor. It can be distinguished from *G. sculleni* by smaller body size, fewer antennomeres, and longer ovipositor. It can be distinguished from *G. gurneyi* by buff yellow dorsal coloration, fewer antennomeres, and longer ovipositor and cerci. It can be distinguished from *G. barberi* by smaller body size, buff yellow dorsal coloration, larger pronotum, and slightly tapered ventral valve of ovipositor. It can be distinguished from *G. chandleri* by having fewer antennomeres, a large, square pronotum with flat posterior edge, and slightly down-curved distal end of the dorsal valve of ovipositor.

Habitat distribution. The type specimen was found on the floor in a dark zone of the main cave system, drowned in a pool of water on June 15, 2010. This pool was located approximately 160 meters from the cave entrance and 43 meters below the surface. This cave is surveyed daily and the specimen was found in good condition (vivid coloration, robust exoskeleton), suggesting that it was freshly deceased. One juvenile specimen used for genetic study was found in the dark zone, drowned in a pool of water on March 20, 2010. Four other juveniles and one penultimate male were found at other times of the year, including November 30, 2006, July 11, 2008, and January 14, 2009. This species is a suspected troglophile, as searches in above-ground habitats surrounding the caves and twilight zones within the caves were unsuccessful.

Geographical distribution. *Grylloblatta oregonensis* **n. sp.** is presently known only from Oregon Caves National Monument (Fig. 3). It may be a limited endemic in this cave system.

Phylogenetic relationships. Based on mitochondrial cytochrome oxidase subunit II data, *G. oregonensis* **n. sp.** (GenBank Accession JN612962) is distinct from (minimum ~10%) other nearby grylloblattids (Table 1). No genetic variation was evident in the two samples. In a neighbor-joining analysis, it is grouped with *G. siskiyouensis* **n. sp.** and *G. marmoreus* **n. sp.** in an unresolved polytomy (Fig. 4).

TABLE 1. Genetic divergence of *Grylloblatta siskiyouensis*, *G. oregonensis*, and *G. marmoreus* from nearby grylloblattid populations. Values are Kimura two-parameter corrected pairwise genetic distance at the cytochrome oxidase II gene. Intraspecific genetic variability, if available, is shown for each species.

Locality	Species	*barberi*	*chandleri*	*chirurgica*	*gurneyi*	*siskiyouensis*	*"rothi"*	*"sculleni"*	*oregonensis*	*marmoreus*
Type	*barberi*	-								
Gray's Flat	*chandleri*	0.1358	-							
Surprise Cave	*chirurgica*	0.2001	0.1649	-						
Type	*gurneyi*	0.1089	0.0719	0.1618	0.00					
Type	*siskiyouensis*	0.1349	0.1275	0.1741	0.1155	0.001				
Mackenzie Pass	*"rothi"*	0.1303	0.1317	0.1737	0.1262	0.1375	-			
Mary's Peak	*"sculleni"*	0.1162	0.1394	0.1874	0.1193	0.1268	0.0734	-		
Type	oregonensis	0.1464	0.1390	0.1870	0.1273	0.1056	0.1597	0.1430	0.00	
Type	marmoreus	0.1357	0.1419	0.1811	0.1279	0.1037	0.1025	0.1507	0.1493	0.004

Grylloblatta siskiyouensis new species

(Figs. 1B, 2C–D)

Type material. Holotype female in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M., Big Tree Loop Trail N42.098 W-123.407 WGS84, Note: near water station 06-III-2007 9:15pm AY SDS10-004" [white label]/ "HOLOTYPE *Grylloblatta siskiyouensis* Schoville det. S.D. Schoville 2011" [red label]; Big Tree Trail of Oregon Caves National Monument, 42.098° North and -123.407° West, Josephine County, Oregon, U.S.A.

Other specimens. Three juveniles in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M., Blind Leads Cave, N42.098 W-123.407 WGS84, 20-III-2010. Note: twilight zone under rocks" [white

label]/ "*Grylloblatta siskiyouensis* Schoville det. S.D. Schoville 2011" [white label]. Two juveniles in ethanol, deposited in CAS, labeled: "USA OR: Josephine Co., Oregon Caves N.M., N42.098 W-123.407 WGS84, 20-III-2010. Note: on snow surface" [white label]/ "*Grylloblatta siskiyouensis* Schoville det. S.D. Schoville 2011" [white label].

Etymology. The specific epithet, *siskiyouensis*, is named for the Siskiyou Mountains in which the type locality, Oregon Caves National Monument, is located.

Diagnosis. Adult females of this species can be distinguished from all other Nearctic *Grylloblatta* species by the following combination of character states: color amber brown on dorsum and white ventrally with light amber yellow patches; small body size; more than 30 antennomeres; ratio of antennomere lengths 2 and 1 1.2; head and interocular distance wider than pronotum; compound eyes large; pronotum short and narrow with a notable point formed at posterior edge; ventral valve of ovipositor broad and slightly up-curved; dorsal valve of ovipositor projects beyond ventral valve one-fifth total length; ovipositor nearly as long as cercus; cercomeres short, distally brown and proximally white.

Description of holotype female. Antennomere number on right antennae 32 and left antennae (broken) 19. Compound eyes well developed, large and black. Interocular distance slightly larger than pronotum width. Head width slightly greater than head length. Pronotum short and narrow, slightly convex, anterior end wider than posterior end, transverse sulcus at anterior end curving slightly towards the posterior end, a weak mid-dorsal line visible, and a notable point formed at the posterior edge. Leg coloration distinctly yellow compared to dorsal body and abdomen, and brown setae distinctive. Ovipositor nearly as long as cercus, extending to eighth cercomere. Ventral valve of ovipositor broad in the middle and slightly up-curved, roughened distally (possible scarring), with noticeable long setae. Dorsal valves of ovipositor extend beyond ventral valve by one-fifth total length and at midpoint nearly straighten out. Cercal segments short, distally brown and proximally white. Dorsal body color amber brown (55), legs light amber yellow (83), abdomen white laterally and light amber yellow patches ventrally, antennomeres and cercomeres amber brown fading to white at distal ends, ovipositor salmon-orange (50).

Measurements of holotype female (cm). BL 1.295, HL 0.294, HW 0.326, EL 0.071, EW 0.0476, ID 0.223, Ant1L 0.0397, Ant2L 0.0476, AntRatio 1.2, PL 0.3176, PW 0.183, FL front 0.333, FL mid 0.397, FL rear 0.508, TL front 0.238, TL mid 0.349, TL rear 0.453, TrL front 0.071, TrL mid 0.103, TrL rear 0.175, PTrL front 0.270, PTrL mid 0.318, PTrL rear 0.318, OvL 0.437, OvW 0.135, CL 0.476.

Description of other specimens. Juveniles are amber brown (55) on the dorsal surface of the head and pronotum.

Comparisons. *Grylloblatta siskiyouensis* **n. sp.** can be distinguished from all *Grylloblatta* species by dark dorsal coloration and dark abdominal color patches, as well as notable point on posterior end of pronotum. It can be distinguished from *G. oregonensis* **n. sp.** by a smaller adult body size and limb length, notably narrower pronotum and head, antennomere count higher (>30) and ratio of antennomere 2:1 lower (<2.0), dorsal valve of ovipositor thicker and slightly more up-curved. It can be distinguished from *G. rothi* by a smaller body size, higher antennomere count (>30), and long, setaceous ovipositor. It can be distinguished from *G. sculleni* by a cercus nearly equal in length to ovipositor. It can be distinguished from *G. barberi* by more reddish dorsal color, narrower head and pronotum, fewer antennomeres, a cercus nearly equal in length to ovipositor, and a less up-curved dorsal valve of ovipositor. It can be distinguished from *G. gurneyi* in having fewer antennomeres and ovipositor nearly equal in length to cercus. It can be distinguished from *G. chandleri* by fewer antennomeres and broader ventral valve of ovipositor.

Habitat distribution. The type specimen was found walking on snow at night in pine forest. I collected two juvenile specimens on the snow at night on March 20, 2010 and three more in the twilight zone of Blind Leads Cave under stones. The adult female specimen examined by Jarvis and Whiting (2006) was collected in a cheese-baited trap near the entrance of a cave.

Geographical distribution. *Grylloblatta siskiyouensis* **n. sp.** is presently known only from Oregon Caves National Monument (Fig. 3). Due to its surface activity, it is potentially more widespread in the Siskiyou Mountains. Kamp (1973) refers to a grylloblattid population near Mt. Ashland that might represent the same species.

Phylogenetic relationships. Based on mitochondrial cytochrome oxidase subunit II data, *G. siskiyouensis* **n. sp.** (GenBank Accession JN612961) is distinct from (minimum ~10%) other nearby grylloblattids (Table 1). This species is represented by the Oregon Caves sample deposited in GenBank (Jarvis & Whiting 2006), from which it differs by a single base (0.1%). In a neighbor-joining analysis, it is grouped with *G. oregonensis* **n. sp.** and *G. marmoreus* **n. sp.** in an unresolved polytomy (Fig. 4).

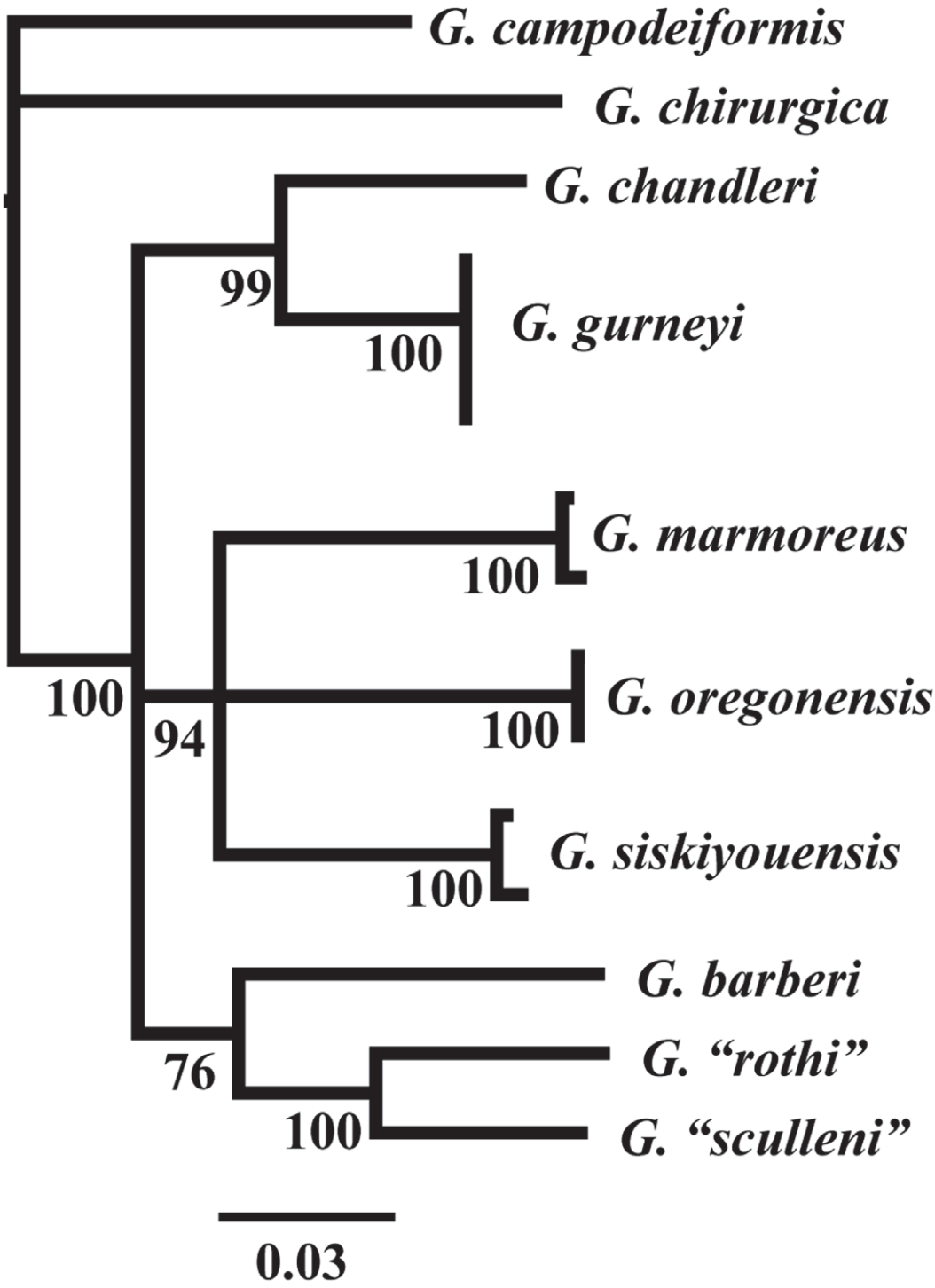

FIGURE 4. Relationships of new *Grylloblatta* species based on mitochondrial cytochrome oxidase subunit II gene data.

***Grylloblatta marmoreus* new species**
(Figs. 1C, 2E–H)

Type material. Holotype male in ethanol, deposited in CAS, labeled: "Big Foot Cave, Marble Mountain Wilderness Area, Siskiyou Co., CA, G.O. Graening & Guy Graening, 3 Sept. 2010" [white label]/ "HOLOTYPE *Grylloblatta marmoreus* Schoville det. S.D. Schoville 2011" [red label]; Big Foot Cave, located in Marble Valley, approximately 41.5628° North and -123.1899° West, elevation 5,935 ft, Marble Mountain Wilderness Area, Siskiyou County, California.

Other specimens. Juvenile in ethanol, deposited in CAS, labeled: "Planetary Dairy Cave, G.O. Graening and David Weaver, 4 July 2010" [white label]/ "*Grylloblatta marmoreus* Schoville det. S.D. Schoville 2011" [white label]; Planetary Dairy Cave, approximately 41.560º North and -123.197º West, elevation 5,621ft, Marble Mountain Wilderness Area, Siskiyou County, California near the headwaters of the Canyon Creek watershed.

Etymology. The specific epithet, *marmoreus*, means "of marble" in Latin and is named for the Marble Mountains of California where this specimen was collected.

Diagnosis. Adult males of this species can be distinguished from those of all other Nearctic *Grylloblatta* species by the following combination of character states: color buff yellow; small body size for genus; relatively short limbs; fewer than 30 antennomeres; ratio of antennomere lengths 2 and 1 1.5; head wider than pronotum; compound eyes well-developed and medium size; pronotum trapezoidal with rounded proximal end and forming soft triangular point at posterior end; subgenital plate with slight rounded tooth; right coxopodite with sharply curved process; left coxopodite with short, stubby stylus; cercus short with short cercomeres.

Description of holotype male. Antennomere count on right antennae 27 and broken left antennae 25. Antennomere 2 1.5X larger than antennomere 1. Compound eyes well developed, length greater along body axis than width, and pigmentation black. Head slightly broader than pronotum but narrower than interorbital distance. Pronotum gently curved in anterior end and triangular at posterior end, overall trapezoidal as width at anterior end greater than posterior end, posterior end forming soft triangular point, transverse sulcus at anterior end curving slightly towards anterior end, length greater than width. Leg coloration amber yellow, slightly lighter than dorsal body color, and small brown setae present. Legs relatively short. Portion of right mid leg below femur removed and destroyed during DNA extraction. Cercus length short with short cercomeres. Subgenital plate more than twice as wide as long, distal edge hardened, distal end forming very slight rounded tooth. Right coxopodite longer than wide with a strong curve towards the ventral side of the body, a short process strongly curved towards anterior on dorsal side near base, stylus borne directly on distal end approximately 30% of the length of coxopodite, and heavily pubescent. Left coxopodite width greater than length, stylus at distal end short and stubby (0.021cm). Dorsal and ventral body color buff yellow (87), appendages lighter amber yellow (83), antennomeres and cercomeres amber yellow fading to white at distal ends, subgenital plate and coxopodites amber yellow.

Measurements of holotype male (cm). BL 1.256, HL 0.228, HW 0.255, EL 0.054, EW 0.034, ID 0.208, Ant1L 0.02, Ant2L 0.03, AntRatio 1.5, PL 0.235, PW 0.214, FL front 0.295, FL mid 0.268, FL rear 0.3886, TL front 0.235, TL mid 0.275, TL rear 0.402, TrL front 0.067, TrL mid 0.1005, TrL rear 0.154, PTrL front 0.201, PTrL mid 0.201, PTrL rear 0.214, SbgL 0.0536, SbgW 0.1273, RCxL 0.1005, RCxW 0.0804, LCxL 0.1139, LCxW 0.134, CL 0.4104.

Description of other specimens. Juvenile specimen is amber yellow (83) on the head and pronotum, with a white abdomen and appendages.

Comparisons. *Grylloblatta marmoreus* **n. sp.** can be distinguished from *G. oregonensis* **n. sp.** in having smaller body size, pronotum narrowing at posterior end and forming soft triangular point, and smaller antennomere 2:1 ratio. It can be distinguished from *G. siskiyouensis* **n. sp.** in having fewer antennomeres, buff yellow coloration and weaker point at posterior end of pronotum. It can be distinguished from *G. rothi* in having a subgenital plate without a lobelike projection on distal end and right coxopodite with a strongly down-curved process. It differs from *G. chandleri* in having a subgenital plate with a more rounded tooth at distal end and right coxopodite with strongly down-curved process. It can be distinguished from *G. sculleni* in having smaller body size and fewer antennomeres; from *G. gurneyi* in having a subgenital plate with a single rounded tooth at distal end and right coxopodite with strongly down-curved process; and from *G. barberi* in smaller body size and having less than 30 antennomeres.

Habitat distribution. The type specimen was found in the twilight zone of a cave habitat, on a rock near ice. The juvenile was found on a rock at the bottom of a pit near the cave entrance.

Geographical distribution. *Grylloblatta marmoreus* **n. sp.** is known from multiple cave sites in the Marble Valley of Marble Mountains, California (Fig. 3).

Phylogenetic relationships. Based on mitochondrial cytochrome oxidase subunit II data, *G. marmoreus* **n. sp**. (GenBank Accession JN612963 & JN612964) is distinct from (minimum ~10%) other nearby grylloblattid species (Table 1). The adult type specimen and the juvenile from Planetary Dairy Cave differ by 0.4%. In a neighbor-joining analysis, it is grouped with *G. oregonensis* **n. sp**. and *G. siskiyouensis* **n. sp**. in an unresolved polytomy (Fig. 4).

Discussion

A century has passed since the first description of *Grylloblatta* in North America (Walker 1914) and the rarity of specimens has posed significant limitations to improving the taxonomic and distributional knowledge of the group. Here I add three new species from a small region in southern Oregon and northern California, two of which are parapatric. The range of *G. oregonensis* **n. sp.** is restricted to the dark portions of cave habitat and G. *siskiyouensis* **n. sp.** is found in the twilight area of the same cave system, as well as nearby surface habitat. Morphological features clearly distinguish these species and genetic data suggest that they are unique evolutionary lineages genetically divergent from other known grylloblattid populations in Oregon and California. While other studies have reported possibly sympatry of North American ice-crawlers (Schoville & Roderick 2010), these results are the first definitive morphological evidence of two species occurring at the same locality. This contrasts with the long-standing view that *Grylloblatta* species are isolated and replace one another ecologically at different sites (Kamp 1979). The phylogenetic analysis suggests that the new species form a monophyletic clade inhabiting the Siskiyou Mountains and Marble Mountains, but does not resolve relationships among the three new species and it does not clarify their relationship to other grylloblattid species groups in California and Oregon. Using additional nuclear data, Jarvis and Whiting (2006) provided evidence that a sample from Oregon Caves, which I have identified as *G. siskiyouensis* **n. sp.**, is basal to almost all other lineages in California and Oregon.

The discovery of grylloblattids in the Marble Mountains extends the distribution of species into the northwest portion of California and raises the possibility of other unknown populations in this region. The geographical distribution of the California species is closely tied to regions of heavy winter snowfall and, as Kamp suggested (1963), to regions in proximity to glacial activity (periglacial habitats). Populations are known from the Sierra Nevada Mountains, east of Mt. Lassen, and in Lava Beds National Monument (Caudell 1924, Gurney 1953, 1961, Jarvis & Whiting 2006, Kamp 1963, Schoville & Roderick 2010). Additional populations are likely to be found in the Klamath mountain region, particularly the Trinity Alps, and might also occur to the southeast on Mt. Shasta and Mt. Eddy. Continued efforts to understand the diversity and evolutionary history of *Grylloblatta* are important, as recent genetic studies have shown that they provide a unique perspective on historical climate changes in California (Schoville & Roderick 2010) and biotic exchange with northeastern Asia (Jarvis & Whiting 2006). These studies provide evidence for several genetically divergent evolutionary lineages that may represent undescribed species in California, Oregon and Washington. Morphological studies are needed to determine the taxonomic status of these lineages, but it seems clear that additional *Grylloblatta* species are likely to be described from the western United States.

It is notable that two of the new species in this study were sampled exclusively from cave habitats, and the third was utilizing the twilight zone of cave habitats. Caves often provide moist, cold microenvironments that are favored by grylloblattids and many grylloblattid populations are known only from caves. However, it is unclear if grylloblattid populations are restricted to the cave environments, or if they are able to use cave ecosystems and surface habitats at different times throughout the year. While behavioral data for most *Grylloblatta* species is lacking (the undescribed species on Mt. Ranier is a notable exception; Edwards 1982), there is evidence that species inhabiting cave habitats in California are active on the surface when snow is present (Schoville 2010, Schoville & Roderick 2010). Furthermore, the morphology of *Gryloblatta* specimens does not suggest morphological changes associated with caves, as compound eyes remain well developed and adults are pigmented. The location of *G. marmoreus* **n. sp.** in the twilight zone near the entrance of caves suggests it may be a trogloxene and simply inhabiting this environment during warm summer months. However, *G. oregonensis* **n. sp.** is known only from collections in the dark zone of caves; it is replaced by *G. siskiyouensis* in surface habitats, and therefore may prove to be limited to cavernicolous environments.

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